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Apogamy in Osmunda cinnamomea and O. Claytoniana

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(WITH 10 TEXT FIGURES)

The occurrence of apogamy in *Osmunda cinnamomea* L. and *O. Claytoniana* L. is of especial interest, since the only reported case of apogamy in this genus is given by Leitgeb.† He does not state definitely in which species he observed apogamy but presumably it was in *O. regalis* L. His observations have never been confirmed, although attempts have been made by workers to induce apogamy in this fern under varied cultural conditions.

The cases of apogamy described in this paper occurred in cultures of *Osmunda cinnamomea* and *O. Claytoniana* with which, together with *O. regalis*, experiments were made during the years 1916–18 in the Osborn Botanical Laboratory of Yale University. The writer is especially indebted to Professor A. W. Evans for many helpful suggestions and criticisms.

MATERIAL

The spores of *O. regalis*, *O. cinnamomea* and *O. Claytoniana* were collected from two sources: from sporophytes growing on lawns about New Haven, Connecticut, and from sporophytes growing under natural environmental conditions in Beaver Swamp, a short distance from that city. No differences were observed in the growth and development of the prothallia from the two sources.

Collections of fertile fronds were made in late June and cultures were made early in July. The cultures were made by sowing the spores on 26 c.c. of Prantl's and Knop's nutrient solutions and their modifications, to which had been added a drop of a 1 per cent solution of ferric chloride, in small glass capsules.

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* Contribution from the Osborn Botanical Laboratory.

† Die Sprossbildung an apogamen Farnprothallien. Ber. Deutsch. Bot. Ges. 3: 169–176. 1885.

The formulas for these solutions are as follows:

I. Prantl's solution (Prantl '81)		II. Knop's solution	
K_2SO_4	0.70g.	$MgSO_4$	0.25g.
NaCl	0.23g.	$Ca(No_3)_2$	1.00g.
$CaSO_4$	0.70g.	K_2HPO_4	0.25g.
$MgSO_4$	0.50g.	KCE	0.12g.
Na_3PO_4	0.50g.		
NH_4NO_3 solution, 0.064 per cent.	20 c.c.		

In the following modified solutions the items not mentioned are the same as in the corresponding unmodified solution:

I. Prantl's solution
I *a*. NH_4NO_3 omitted
I *b*. K_2SO_4 omitted
I *c*. NaCl omitted
I *d*. $CaSO_4$ omitted
I *e*. $MgSO_4$ omitted
I *g*. NaCl and Na_3PO_4 omitted

II. Knop's solution
II *a*. $Ca(NO_3)_2$ omitted

After the spores had been sown the cultures were placed before an east window and the culture solutions were not renewed. It was only during the period of germination that the cultures were exposed to the direct rays of the sun for a short time each day. If left longer the solution became heated and the prothallia died.

Development of prothallia and sex organs

Germination, in all three species, began in a few days after the spores were sown.

O. regalis.—Three weeks later the prothallia of this species varied in the different cultures from four to fifty-nine cells, the greatest irregularity in size occurring in cultures of I*c*. On the whole greater growth occurred in cultures of the modified than in those of the unmodified solutions, and this was especially true in the case of I*a*. Here the amount of nitrate present was evidently sufficient to meet the needs for the growth of the prothallia and the effect of the unbalanced solution tended at first to stimulate rather than retard the growth. However, the reverse was true in the later development of the prothallia, for at the end of the fourth month in I*b*, I*c*, I*d*, Ig, and II*a* the majority of the prothallia were dead; in I*a*, I*f*, and I*g*, although the prothallia were alive, growth was much slower.

Campbell* states, "in . . . *O. regalis* it is quite common to have the first transverse wall followed by a longitudinal wall in each cell, so that the four primary cells are arranged quadrantwise." While in general this was the order of development, yet in some of the cultures a filamentous stage of two and three cells was formed before longitudinal division took place. Even in those cases where the four primary cells were arranged quadrantwise the prothallia tended to assume an elongated form and not a cell mass at first. In I*d* the prothallia were very broad and frequent branching occurred at the expanded apices of the prothallia. In I*e* and I*f* the growth was very irregular, some of the prothallia tending to assume an elongated form and others a broad form. Branching in these cultures was rare; in I and II*a*, however, it was common, the branches often occurring as filamentous outgrowths at the bases of the young prothallia, which were decidedly filamentous in form. In some cases this was so marked that a reversion of the prothallia at its apex to a filamentous condition took place. Large heart-shaped prothallia, monoecious in most cases, were present in the unmodified solutions. No cases of apogamy in the species were observed.

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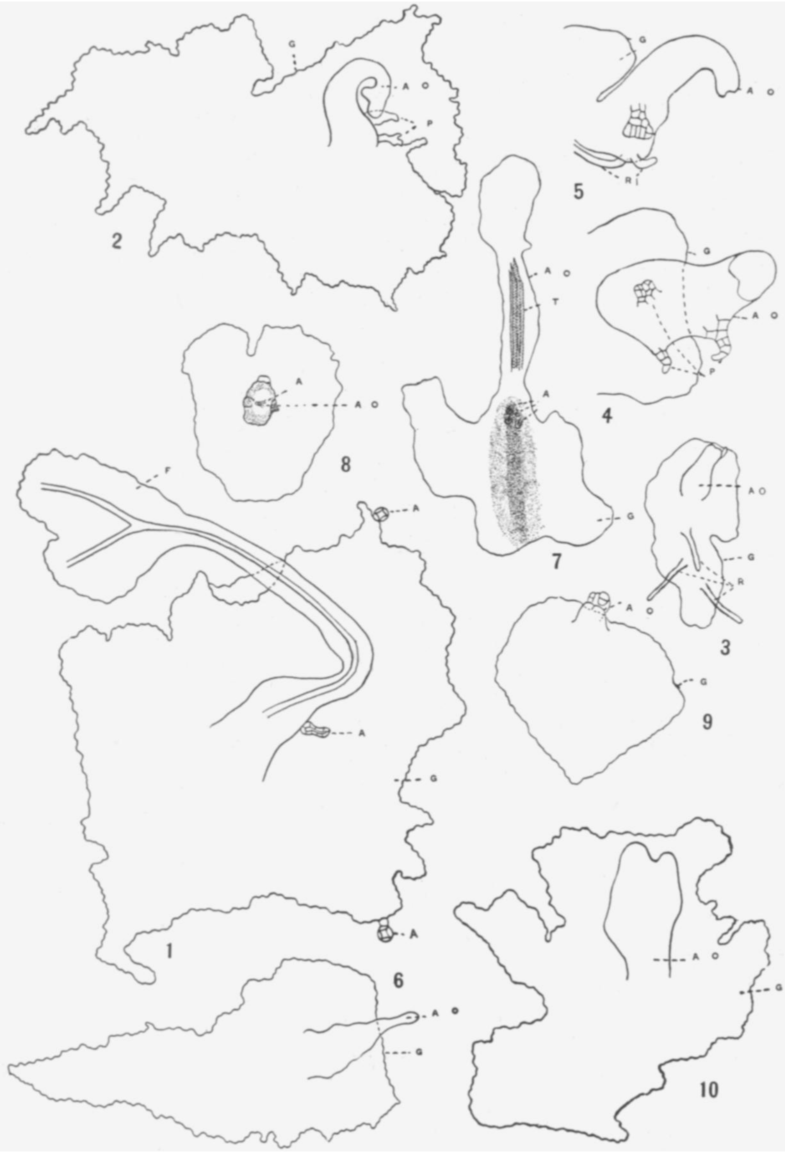
* Mosses and Ferns, p. 340. London. 1895.

O. cinnamomea.—Growth in this species during the first three weeks was not so rapid as in *O. regalis*, for the largest prothallia were only thirty-four cells in size and the smallest two cells. As in *O. regalis* greatest growth took place in I*a*, while least growth occurred in I*b* and I*f*. The early divisions of the prothallia were in keeping with the previously quoted statement of Campbell. However, in many cases in I*a* the filamentous stage consisted of from three to five cells. The young prothallia in most of the cultures were broad in form, sometimes a mere cell mass. In the case of the prothallia in II (Knop's unmodified solution), while the initial divisions were the same, there was more of a tendency for the young prothallia to become elongated and in rare cases a filamentous stage, as many as seven cells in length, was formed before longitudinal divisions took place.

A greater irregularity in the form of the young prothallia occurred in the cultures of the various modified solutions than in the same cultures of *O. regalis*. In I*a*, I*c*, I*d*, I*f* and I*g* the form of the young prothallia was very irregular, this being especially pronounced in I*a* and I*c*. Greater regularity of form occurred



FIGS. 1–7. Apogamous outgrowths of *Osmunda cinnamomea*. FIGS. 8–10. Apogamous outgrowths of *Osmunda Claytoniana*. *AO*, apogamous outgrowths; *a*, archegonia; *a′*, antheridia; *f*, leaf; *g*, gametophyte; *r*, rhizoid, *t*, tracheids.

in I*b* and I*e*. In II*a* the regularity of form was very striking. However, at the end of eight months the greatest irregularity of form was shown by the prothallia of I*a* and I*c*. Many of these were elongated plates of cells with the margins of the apices extremely irregular. Branching of the prothallia occurred in the cultures of the following solutions: I*a*, I*b*, I*c*, I*d*, I*e* and I*g*, being especially marked in I*a*, I*b*, I*c* and I*d*.

Sexual organs, both male and female, developed in various cultures. That some of these were normal was shown by the presence of young sporophytes, which developed only in the unmodified solutions after the nutrient solution had been renewed.

Apogamous outgrowths, developed on prothallia in cultures of the following solutions, eight months and one week (March 9, 1917) after the spores were sown (FIGS. 1–6): I, I*a*, I*b* and I*e*. In another attempt to induce apogamy, prothallia were transferred from cultures of I (Prantl's unmodified solution) to I*a* four weeks after the spores were sown. One case of apogamy in these cultures was observed (FIG. 7).

O. Claytoniana.—At the end of three weeks the average size of the prothallia of this species in the different cultures varied from one to thirty-three cells. As in *O. regalis* and *O. cinnamomea* the greatest growth occurred in I*a*; least growth occurred in I*c*. No filamentous stage was present in many of the prothallia of the unmodified solutions, a longitudinal wall having been formed in the first cell. In other prothallia the filamentous stage varied from five cells in I*c* and I*f* to six cells in II*a*, seven cells in I*c* and II*a* and eight cells in I*c*.

The young prothallia in the cultures of the unmodified solutions I and II and the modified solutions I*a*, I*b*, I*c*, I*g* and II*a* were regular in form, being somewhat elongated. But in I*d*, I*e*, I*f* and II*a* the form of the majority of the prothallia was very irregular; in some cases they were broad, in others elongated. The older prothallia (March 19, 1917) in the cultures of I*a*, I*b*, I*d*, I*g* and II*a* showed the greatest irregularity of size and form. Those of I*d* and I*g* were the smallest in size, while those of I*a* and I*b* were the most irregular in form, some of the prothallia of I*a* being irregular plates of cells.

No branching of the prothallia was observed in the cultures of I*b* and II while in I, I*a*, I*c*, I*d*, I*e* and I*f* it was rare. In the cultures of I*g* branching of the prothallia was very common. In all cases observed the branching of the prothallia occurred in the younger stages of the development.

Sexual organs were found in the unmodified solutions, while in the modified solutions they were formed only on the prothallia in I*a* and I*b*. However, in the latter only a few sexual organs were observed. Normal sporophytes developed in some cultures of the unmodified solutions after the nutrient solutions had been renewed, and three apogamous outgrowths occurred on prothallia in I*b* (FIGS. 8–10).

DESCRIPTIONS OF THE APOGAMOUS OUTGROWTHS

The apogamous outgrowths in *O. cinnamomea*, as previously stated, developed on prothallia in cultures of I, I*a*, I*b* and I*e*. One developed also on a prothallium which had been transferred from I (Prantl's solution), four weeks after the spores were sown, to I*a*.

The prothallium in a culture of I (FIG. 1), upon which the apogamous outgrowth occurred, was irregular in shape and no sinus was present. Two antheridia developed from marginal cells, one in the expanded apex and one near the base of the prothallium. One of the antheridia was stalked and the other sessile. The prothallium was one cell thick, except for a small region in the center where the meristem is usually formed. In this region a swelling occurred which continued to grow, forming a cylindrical process several cells in thickness. Gradually it assumed the shape of a young leaf and finally developed into a normally appearing leaf consisting of a petiole and a blade bearing a forking rib. On one side of the petiole near its enlarged base an archegonium which appeared normal developed.

The apogamous outgrowth which occurred in a culture of I*a* developed in the same manner as the one just described. This prothallium, also, was approximately the same size and shape (FIG. 2); however, no antheridia or archegonia were formed.

The apogamous outgrowth found in a culture of I*b* developed on a prothallium which was small, elongated and regular in shape. No sinus was present and from the meristematic region near the apex of the prothallium the apogamous outgrowth was formed. It began as a swelling which developed into a cellular mass.

Swollen at its base it narrowed and then enlarged into an apex which was slightly lobed (FIG. 3). This structre continued to elongate and formed a flat, cellular mass which was lobed (FIGS. 4, 5). From near its base and on one side of the structure proliferations of a thallus-like character developed.

The prothallium in the culture of I*e*, which gave rise to the apogamous outgrowth, was wedge-shaped with an obtuse apex without a sinus (FIG. 6). As in the previous cases described the apogamous outgrowth developed as a swelling from the meristematic region. This swelling continued to grow, forming a cylindrical process several cells in thickness which became somewhat narrower as it developed.

An apogamous outgrowth formed on a prothallium which had been transferred from I to I*a*, four weeks after the spores were sown. This prothallium (FIG. 7) was broad and irregular, one lobe being much larger than the other. A meristem was present from which archegonia, normal in appearance, developed. From the margin of the prothallium, where the sinus is usually formed, the prothallium continued to grow into a cylindrical cellular structure, which finally broadened into a flat thallus-like body one cell in thickness with a rounded apex. Tracheids were formed in the narrow thickened portion.

All three cases of apogamy in *O. Claytoniana* were observed in cultures of I*b*, where they developed as cellular masses on the prothallia (FIGS. 8–10). One of these cellular masses, formed as a swelling from the meristem near the center of a heart-shaped prothallium which was distinctly notched, bore on the side near its apex an archegonium (FIG. 8). Another of these cellular masses (FIG. 9) was formed a little to one side of the center of the meristem and near the expanded apex of a prothallium. This outgrowth began as a swelling of the tissue, which was triangular without a sinus, and developed into a mass whose apex was slightly lobed. From one side a proliferation of a thallus-like character developed. The third cellular mass was formed on a very irregular prothallium (FIG. 10). Although the margin was greatly indented in places no apica sinus was present. The apogamous outgrowth, as in the other two cases, appeared first as a swelling of the meristem and then developed into an irregular, cylindrical cellular mass whose apex was distinctly bilobed.